

A STUDY OF VARIATION IN THE CYTOTYPES OF DRYOPTERIS SPINULOSA.

ROLLA TRYON¹ AND DONALD M. BRITTON²

Among the groups of ferns in which cytological and evolutionary studies are being pursued most vigorously is the genus *Dryopteris* (*sens. strict.*) of North America and Europe. In eastern North America (see Bibliography) thirteen fertile cytotypes have been recognized, and among these six are diploid ($n=41$), six are tetraploid and one is hexaploid. Sixteen sterile hybrids of these fertile cytotypes have been examined cytologically and four of them are diploid, nine are triploid, two are tetraploid and one is pentaploid. These previous studies have been concentrated on chromosome counts of the taxa and hybrids to determine the level of ploidy and on chromosome pairing analyses of natural and synthetic hybrids as evidence of their genome relations. There have been no extensive cytological surveys of any of the cytotypes nor analyses of their variation. It was against this background, and our belief that cytological data can be fully exploited in evolutionary studies only when accompanied by data on morphological variation, that the present work was initiated. The data that we have obtained on variation of the cytotypes of *Dryopteris spinulosa* is pertinent to the problem of the origin of the tetraploid var. *spinulosa* and to the problems of the evolutionary potential of triploids and the variation of derived hexaploids.

Dryopteris spinulosa var. *intermedia* (2 X) and var. *spinulosa* (4 X) were chosen as especially suitable taxa for investigation because of their abundance and because of the abundance of their sterile triploid hybrid. These taxa presented an opportunity to study and compare variation, in a related diploid and tetraploid and their hybrid, on a broad

¹Gray Herbarium, Harvard University.

²Department of Botany, University of Guelph. This study was supported, in part, by grants from Sigma Xi-RESA to D. M. Britton.

basis. *Dryopteris spinulosa* is a rather common species in northeastern United States and adjacent Canada where it usually grows on wooded hillsides, or in wooded swamps and less often in shrubby swamps, or along damp roadsides. Variety *spinulosa* (figs. 9, 10) grows more commonly in wet, often water-logged sites, while var. *intermedia* (figs. 5,

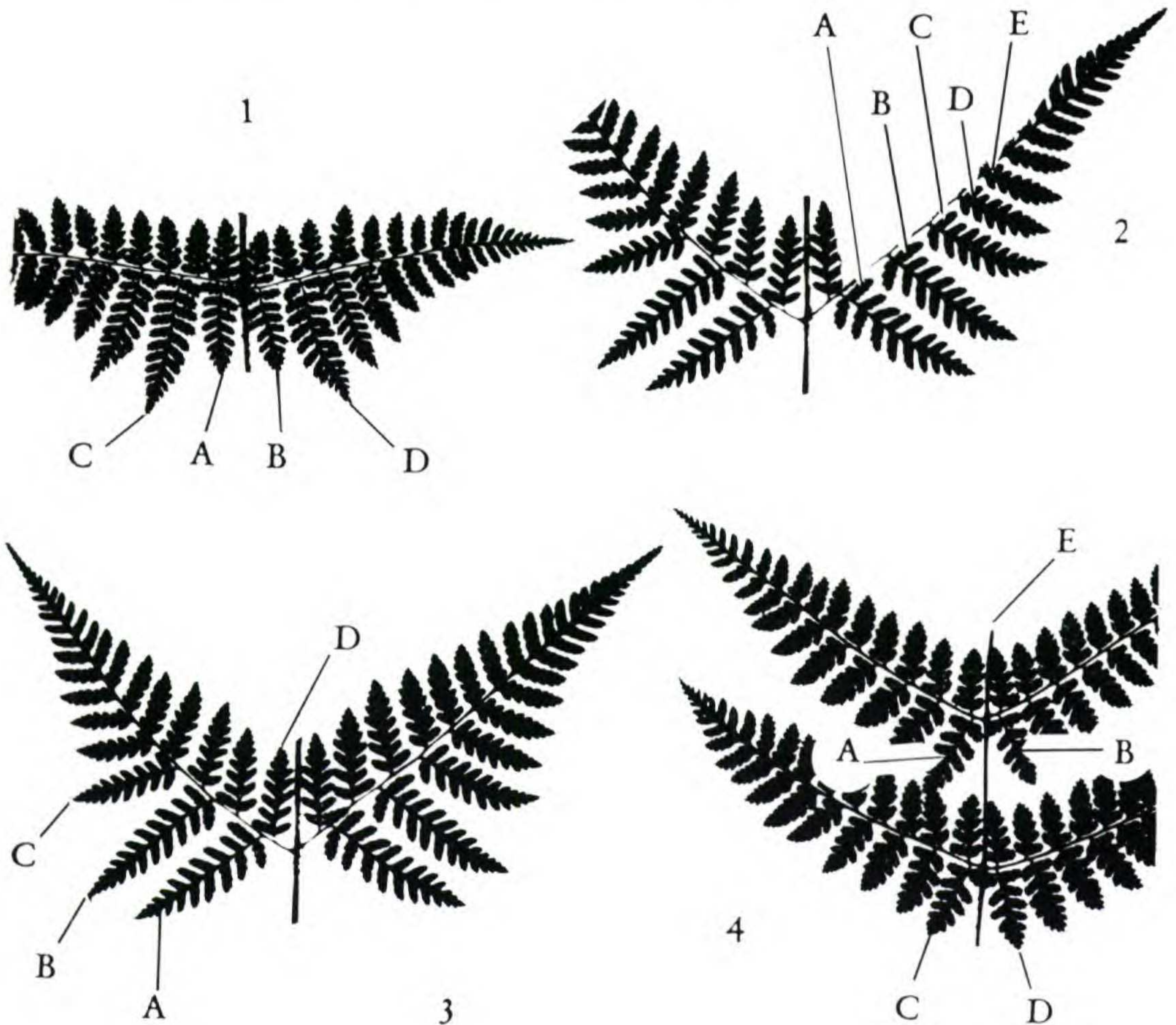


PLATE 1320

Figs. 1-4. Illustrations of characters *c* to *f*. Fig. 1 — character *c*, basal pinnae of *intermedia*, each inferior basal pinnule, A and B, is shorter than the adjacent one, C and D. Fig. 2 — character *d*, basal pinnae of the *hybrid*, five basal tertiary segments, A to E, on the acroscopic side of the inferior pinnules, are parallel to the pinna-rachis. Fig. 3 — character *e*, basal pinnae of the *hybrid*, three of the inferior pinnules, A to C, are longer than the basal superior pinnule, D. Fig. 4 — character *f*, central pinnae of *intermedia*, on each of the four pinnae, the basal inferior pinnule, A to D, overlies the rachis, E.

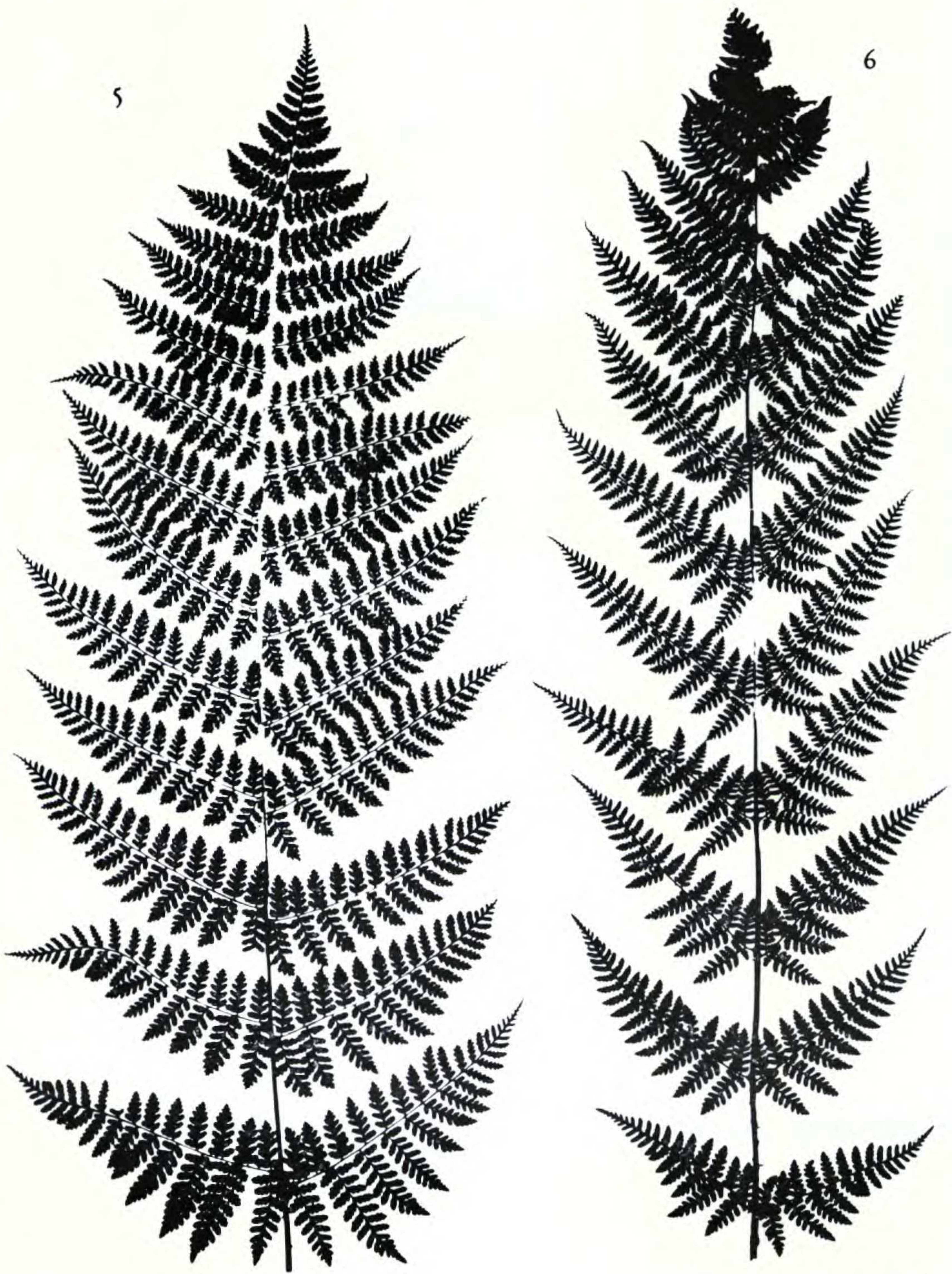


PLATE 1321

Figs. 5-6. Lamina of *Dryopteris spinulosa* var. *intermedia*, diploid, $\times \frac{1}{4}$. Fig. 5 — from Plant 110. Fig. 6 — from Plant 357.

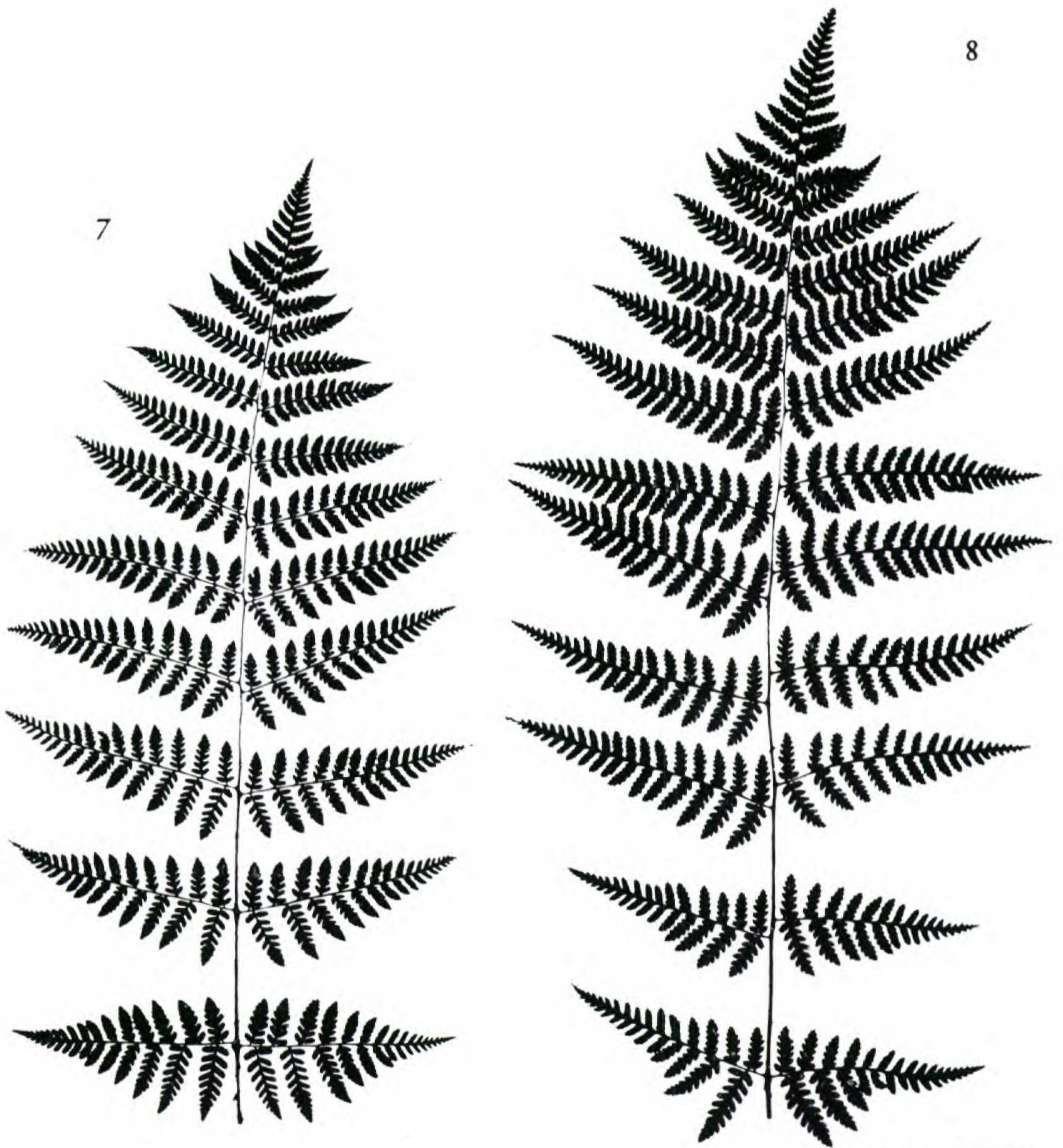


PLATE 1322

Figs. 7-8. Lamina of *Dryopteris spinulosa* var. *intermedia* \times var. *spinulosa*, triploid, $\times \frac{1}{4}$. Fig. 7— from Plant 487. Fig. 8— from Plant 268.

6) is most often in moist but well drained sites, but both exhibit considerable latitude in their habitat. The two varieties frequently grow intermixed or in close proximity to each other. In our experience, their hybrid (figs. 7,8) is found whenever the two parents are in some abundance (and sometimes when one is rare) and it is usually frequent or even more abundant than either parent.

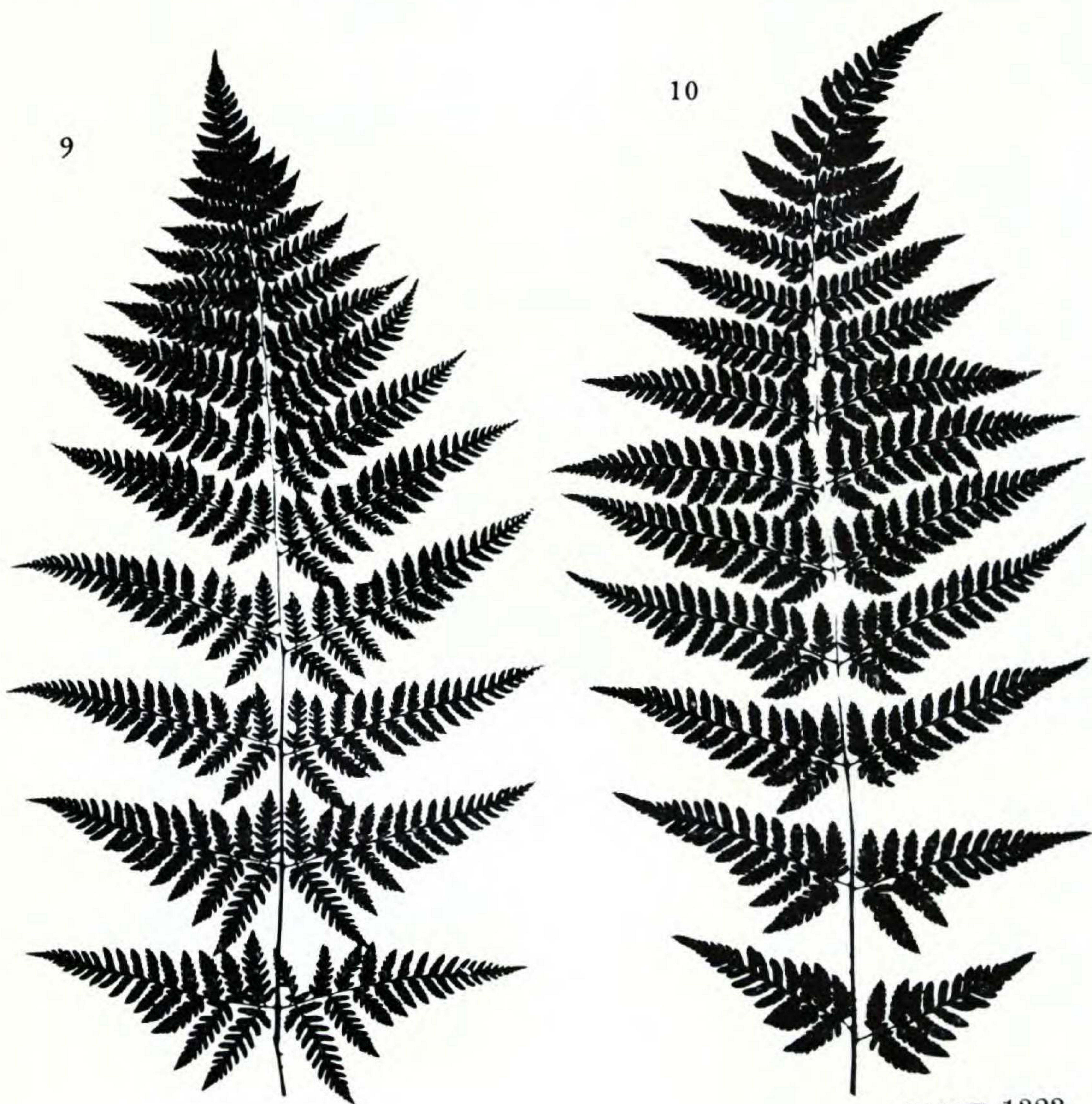


PLATE 1323

Figs. 9-10. Lamina of *Dryopteris spinulosa* var. *spinulosa*, tetraploid, $\times \frac{1}{4}$. Fig. 9 — from Plant 272. Fig. 10 — from Plant 294.

The classification and nomenclature of this group is subject to considerable uncertainty and disagreement. While this paper does not intend to deal with either of these matters in a definitive manner, we do present some reasons later for the classification adopted. It is well established that var. *spinulosa* and var. *intermedia* are taxa (major evolutionary units) and disagreements about their taxonomic rank is of secondary importance. Some of the difficulties involved in the correct nomenclature are so involved and technical that we wish to do no more than mention their

existence. The following synonymy will serve to orient the reader with other names currently used for these plants.

Dryopteris spinulosa (O. F. Muell.) Watt, var. **spinulosa** (*Dryopteris spinulosa*; *Dryopteris spinulosa*, "typical"; *Dryopteris austriaca* (Jacq.) Woynar, var. *spinulosa* (Muell.) Fiori). In the remainder of the paper this will be referred to as *spinulosa*.

Dryopteris spinulosa var. **intermedia** (Willd.) Underw. (*Dryopteris intermedia* (Willd.) A. Gray; *Dryopteris austriaca* var. *intermedia* (Willd.) Morton). In the remainder of the paper this will be referred to as *intermedia*.

Dryopteris spinulosa var. **intermedia** × var. **spinulosa** (*Dryopteris intermedia* × *spinulosa*; *Dryopteris spinulosa* var. *fructuosa* (Gilbert) Trudell; *Dryopteris austriaca* var. *fructuosa* (Gilbert) Morton; *Dryopteris* × *triploidea* Wherry). In the remainder of the paper this will be referred to as the *hybrid*.

This study was initiated in 1959 and has continued through June of 1965. Rolla Tryon has made the analyses of the characters, Donald M. Britton the cytological determinations and the collections of specimens; both have contributed to the discussions and conclusions.

MATERIALS AND METHODS OF STUDY.

Most of the plants used in this study (155) were obtained from southern Ontario (west of 79° W. Long. and south of 46° N. Lat.). Twenty-five others were from the Algoma District of Ontario (east of Lake Superior) and eight were from Pennsylvania and Virginia. The material for cytological study was usually collected in late May to the middle of June. At that time a voucher leaf was taken from the plant and prepared as an herbarium specimen. In many cases, the plant also was marked with the collection number and additional leaves were collected from some of these plants in September of the same year and also in the following year. Individual plants, therefore, have been represented by one to sixteen leaves and often by sets of leaves collected in successive years. Eighty-nine plants of *intermedia* were determined as diploid ($n=41$); forty-seven plants of the *hybrid* were determined as triploid ($n=123$);

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and fifty-two plants of *spinulosa* were determined as tetraploid ($n=82$). Voucher specimens of these cytologically

determined plants have been deposited in the Herbarium, Department of Botany, University of Guelph and a selection of them in the Gray Herbarium, Harvard University.

Not all of the 188 plants and 746 leaves available have been used in this study. Some leaves were defective and others were too small (less than 25 cm. long) to be included in case they would bias the results. About 175 plants and 550 leaves were available for most characters; the number studied for each is given as part of Charts 1 and 2.

Thirty-four characters were considered during the course of our work. Eleven of these were studied in some detail and the results of these analyses are presented. Preliminary studies were made of eighteen other characters but these were not continued because the characters were either too variable to be of particular value or because no significant differences between *spinulosa* and *intermedia* were observed. Among these, a few of the variable characters were the following: complexity of the lamina, shape of the pinnae, tapering of the apex of the pinnae and size of the indusium. The variation of four other characters was not analysed principally because of technical difficulties in their study. An initial survey of these indicated that they probably behaved in the same manner as some of the characters analyzed in detail. These characters were the orientation of the rhizome, the color of the petiole scales, the evergreen quality of the leaves and the kind of habitat. Finally, the apex of the spines of the spores was not studied simply because of the small size of the character, the spines themselves being only about 1 micron long.

The illustrations have been prepared from a selection of specimens of the cytologically determined plants. These specimens were photographed and the negative printed as a silhouette. The specimens were relaxed in warm water, prior to photographing, so that they were substantially restored to their fresh condition. This is of some importance because minor shrinking, wrinkling and curling of the teeth and ultimate lobes can alter the total aspect of a pinna or lamina to a considerable degree.

ANALYSIS OF CHARACTERS.

The following comments on the individual characters explain the character, when necessary, and the manner in which it was studied. The original measurements or counts for six of the characters are presented in Charts 1 and 2 and in Graph 1. In order to compare the range of variation of the different characters and their means, this data was adjusted to a scale of 0 to 100 for each character (the minimum count or measurement=0, the maximum=100). For example, character *e* varies from a minimum count of 1 to a maximum of 8. Then 1=0 and 8=100 and counts of 2 to 7=14, 28, 43, etc., respectively. For characters *b* and *c* the score was then reversed (0=100, 100=0) so that the scores for all of the characters would be high for *intermedia* and low for *spinulosa*. These adjusted scores are presented in Chart 3 and in Graph 2. Selections of the data are presented in Charts 4 and 5 and in Graph 3 to illustrate special features of the variation of the cytotypes.

a. Glandularity of the base of the pinna.

The lamina of *intermedia* is glandular while that of *spinulosa* is usually glabrous. The glands are small, stalked and have a more or less spherical cap cell. They are usually most abundant at the base of the pinnae. There is some tendency for them to be deciduous as the leaf ages, although they will persist on leaves that have lived over the winter. In order to obtain a measurement of this character, the cytological voucher leaves (collected in early summer) were used and a single central pinna was chosen for observation. The glands that could be seen on the lower surface on one linear millimeter of the pinna stalk were counted. The data obtained from sixty plants are presented in Chart 1.

b. Length of the guard cells of the stomata.

This character was studied only in a preliminary manner although the results indicate that extended data would be of much interest. A portion of a leaf collected in late summer was relaxed in warm water and then placed in a lactic acid mount. Measurements were made, in micra, of the maxi-

mum length of the guard cells from stomata between the veins on the lower surface and the mean from ten measurements was obtained for each leaf. The data obtained from 27 plants are presented in Chart 1.

c. Length of the inferior basal pinnules on the basal pinnae in relation to the adjacent ones.

Each basal pinna of *intermedia* usually has the inferior basal pinnule shorter than the adjacent one (fig. 1), while *spinulosa* usually has the inferior basal pinnule longer than the adjacent one (fig. 16).

CHART 1. Analysis of variation in *Dryopteris spinulosa*, original counts and measurements of characters *a* and *b*. (See Graph 1.)

Range of variation of Mean of all leaves.
all leaves.

(Total number of leaves.)

a. Glandularity of the base of the pinna: number of glands on one linear mm. of pinna-stalk, each leaf from a different plant.

| | | |
|-------------------|---------------|------|
| <i>intermedia</i> | 10-75 (20) | 45.6 |
| <i>hybrid</i> | 9-55 (20) | 29.2 |
| <i>spinulosa</i> | 0-9 (20) | 1.6 |

b. Length of the guard cells of the stomata: mean of ten measurements for each leaf, each leaf from a different plant.

| | | |
|-------------------|--------------------|------------|
| <i>intermedia</i> | 34-53 micra (9) | 42.5 micra |
| <i>hybrid</i> | 40-58 micra (9) | 49.5 micra |
| <i>spinulosa</i> | 44-68 micra (9) | 55.7 micra |

The character was measured by taking the average of the length of both basal pinnules and both adjacent ones because the relative length of these two pinnules may differ on each basal pinna. The measurements are in millimeters and the average is expressed as the basal pinnules being longer, or shorter, than the adjacent ones. The data obtained from 546 leaves are presented in Chart 2; illustrations of the variation are given in figs. 11-16.

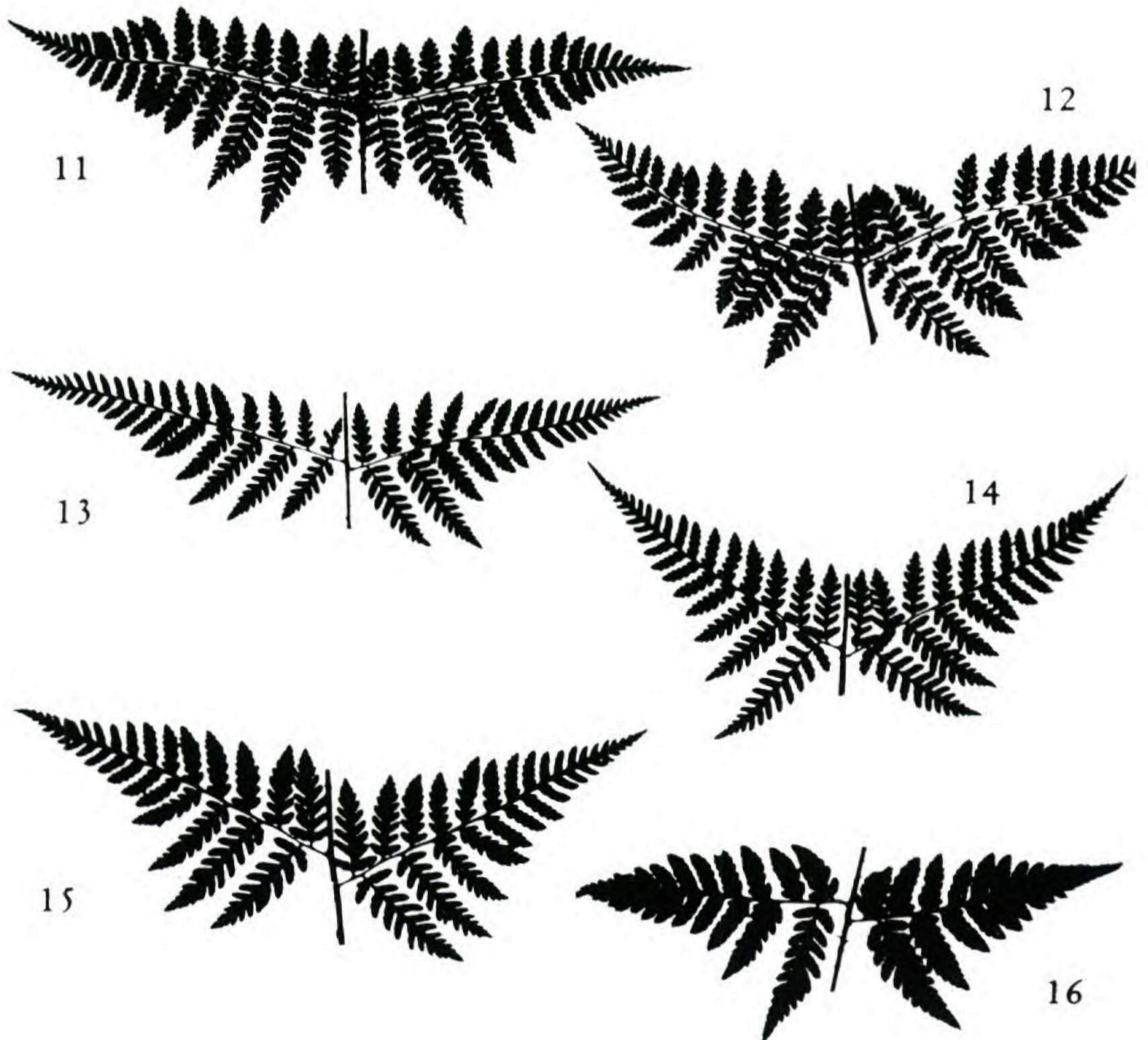


PLATE 1324

Figs. 11-16. Basal pinnae, $\times 1/3$. Figs. 11-12. *Dryopteris spinulosa* var. *intermedia*, diploid. Fig. 11 — from Plant 28, the inferior basal pinnules are 15 mm. shorter than the adjacent ones. Fig. 12 — from Plant 110, the inferior basal pinnules are 7 mm. longer than the adjacent ones. Figs. 13-14. *Dryopteris spinulosa* var. *intermedia* \times var. *spinulosa*, triploid. Fig. 13 — from Plant 38, the inferior basal pinnules are 7 mm. shorter than the adjacent ones. Fig. 14 — from Plant 502, the inferior basal pinnules are 10 mm. longer than the adjacent ones. Figs. 15-16. *Dryopteris spinulosa* var. *spinulosa*, tetraploid. Fig. 15 — from Plant 68, the inferior basal pinnules are equal in length to the adjacent one. Fig. 16 — from Plant 36, the inferior basal pinnules are 15 mm. longer than the adjacent ones.

d. Number of parallel tertiary segments.

In *intermedia* there is a strong tendency to have many of the basal tertiary segments, on the acroscopic side of

the pinnules, disposed more or less parallel to the pinna-rachis. This character is illustrated (by the *hybrid*) in fig. 2. In *spinulosa* (fig. 15) there is a strong tendency to have rather few such segments parallel to the pinna rachis. This character has been counted on one arbitrarily chosen basal pinna and on the pinnules on its inferior side, as illustrated in fig. 2. The data obtained from 565 leaves are presented in Chart 2.

This character may be correlated with the size of the pinna and for this reason small leaves were not used in its study. In leaves of moderate or large size there is no absolute correlation with the size of the pinna as the following counts will show. In a plant of *spinulosa*, a basal pinna of one leaf was 9.5 cm. long and had 1 parallel tertiary segment on its inferior side. A basal pinna, from another leaf of the same plant, was 8 cm. long and had 2 parallel tertiary segments on its inferior side.

e. Number of longer inferior pinnules.

The pinnae in *spinulosa* tend to be relatively broad at the base and to be abruptly reduced in width. In *intermedia* there is a tendency for the pinnae to be hardly, or not at all, broadest at the base and to be gradually reduced in width. These tendencies have been reduced to an easily observed character by using one basal pinna and comparing the length of the inferior pinnules with the basal superior one. The character was taken from the basal pinna with the shortest basal superior pinnule and, in reference to this pinnule, the number of inferior pinnules that were longer was determined. The data obtained from 546 leaves are presented in Chart 2; and the character is illustrated (by the *hybrid*) in fig. 3.

As in the study of the previous character, small leaves were not used because of the possibility that small pinnae would bias the data. In leaves of moderate to large size, there is no absolute correlation with the size of the pinna as the following counts will show. A basal pinna of one leaf of a plant of *intermedia* was 11.5 cm. long and had 5

longer inferior pinnules. A basal pinna from another leaf of the same plant was 10 cm. long and had 6 longer inferior pinnules.

CHART 2. Analysis of variation in *Dryopteris spinulosa*, original counts and measurements of characters *c* to *f*. (See Graph 1.)

| | Range of variation | | Mean of all leaves. |
|---|--|---|---------------------|
| | All leaves. (Total number of leaves.) | Plant means from plants with 4 or more leaves. (Total number of plants: total number of leaves.) | |
| <i>c.</i> Length of the inferior basal pinnules of the basal pinnae in relation to the adjacent ones. | | | |
| <i>intermedia</i> | 16 mm. shorter to 7 mm. longer. (255) | 10 mm. shorter to 2 mm. longer. (31: 172) | 4.5 mm. shorter |
| <i>hybrid</i> | 7 mm. shorter to 11 mm. longer. (119) | 1.5 mm. shorter to 5 mm. longer. (16: 87) | 1.7 mm. longer |
| <i>spinulosa</i> | equal to 16 mm. longer. (108) | 3.7 mm. longer to 9 mm. longer (11:60) | 6.4 mm. longer |
| <i>d.</i> Number of parallel tertiary segments. | | | |
| <i>intermedia</i> | 3-10 (296) | 4.0-6.8 (19: 107) | 5.7 |
| <i>hybrid</i> | 1-8 (137) | 2.5-4.7 (18: 95) | 3.4 |
| <i>spinulosa</i> | 1-5 (132) | 1.6-3.5 (14: 82) | 2.5 |
| <i>e.</i> Number of longer inferior pinnules. | | | |
| <i>intermedia</i> | 2-8 (278) | 3.4-6.2 (34: 212) | 4.8 |
| <i>hybrid</i> | 2-5 (135) | 2.0-3.6 (17: 96) | 2.9 |
| <i>spinulosa</i> | 1-4 (133) | 2.0-3.1 (14: 84) | 2.1 |
| <i>f.</i> Number of pinnules that overlie the rachis. | | | |
| <i>intermedia</i> | 0-10 (299) | 1*-2.9-10 (30: 162) | 7.8 |
| <i>hybrid</i> | 0-7 (155) | 0-3.0 (20: 107) | 1.0 |
| <i>spinulosa</i> | 0-3 (138) | 0-0.75 (17: 97) | 0.07 |

*Plant 357 with two leaves.

f. Number of pinnules that overlie the rachis.

In *intermedia*, the pinna, the basal inferior pinnule and its basal segment nearest the rachis are disposed so that the basal segment is relatively close to the rachis and most often so that it overlies it (figs. 4 and 5.). In *spinulosa* these same structures are disposed so that the basal segment is relatively far from the rachis (figs. 9 and 10). This character was analyzed by the number of basal inferior pinnules that overlie the rachis on the lowest ten pinnae. Fig. 5 shows a lamina with 10 overlying pinnules and figs. 9 and 10 show laminae with no overlying pinnules. Only 10 pinnae were used in order to avoid bias due to high counts in unusually large leaves. Bias due to low counts in small leaves was eliminated (or reduced) by taking only those leaves with a lamina at least 30 cm. long. In order to confirm that this character was not related to changes in orientation due to pressing of the leaf, counts were made on the same leaves when they were fresh and after they were pressed. No difference was observed. The data obtained from 592 leaves are presented in Chart 2.

g. Position of the pinnae in relation to the rachis.

The pinnae may be patent (more or less at right angles to the rachis) or they may vary to ascending (at an acute angle to the rachis). This character was originally studied because it has been one that has been prominently used for the identity of the taxa, and especially of the *hybrid*. However, so much variation was soon observed in both *intermedia* and *spinulosa* that the character was neither studied further nor refined. Figures 17 and 18 of *intermedia* and figs. 31 and 32 of *spinulosa* illustrate some of the variation observed in the pinna-angle. Ninety-seven leaves of *intermedia* had patent pinnae, 55 leaves had them slightly ascending and 23 had them definitely ascending. The same range of variation, but in somewhat different proportions, was seen in *spinulosa* in which 13 leaves had patent pinnae, 47 leaves had slightly ascending pinnae and 23 leaves had definitely ascending pinnae. The character was also studied on plants from which several leaves were available but these

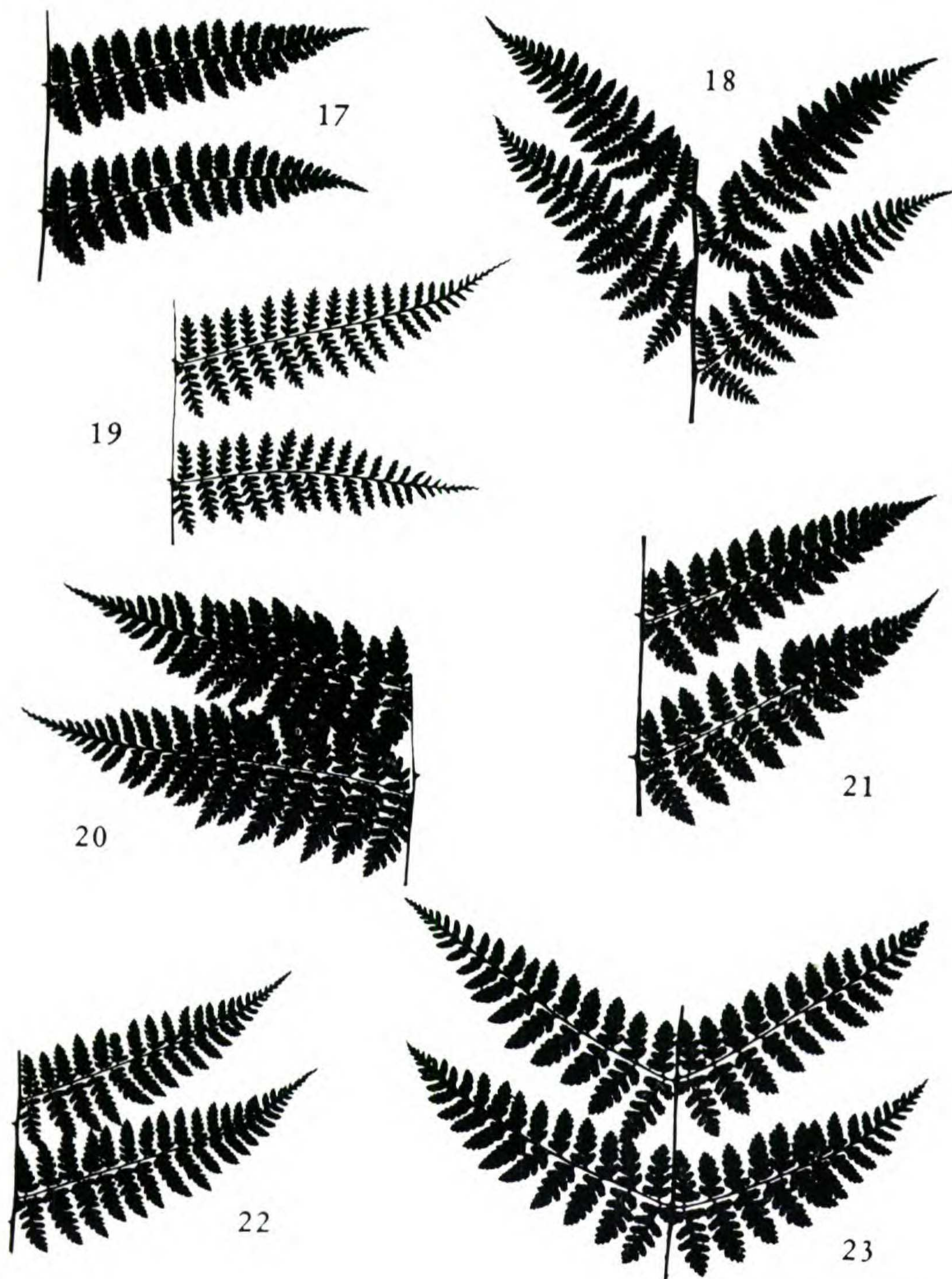


PLATE 1325

Figs. 17-23. Central pinnae of *Dryopteris spinulosa* var. *intermedia*, diploid, $\times 1/3$. Fig. 17 — from Plant 105. Fig. 18 — from Plant 357. Fig. 19 — from Plant 335. Fig. 20 — from Plant 108. Fig. 21 — from Plant 29. Fig. 22 — from Plant 104. Fig. 23 — from Plant 111.

results confirmed the previous data, i.e., although there was a slight statistical difference between *intermedia* and *spinulosa* it was not a sufficient one to invite further analysis.



PLATE 1326

Figs. 24-29. Central pinnae of *Dryopteris spinulosa* var. *intermedia* × var. *spinulosa*, triploid, × 1/3. Fig. 24 — from Plant 86. Fig. 25 — from Plant 84. Fig. 26 — from Plant 562. Fig. 27 — from Plant 87. Fig. 28 — from Plant 338. Fig. 29 — from Plant 32.

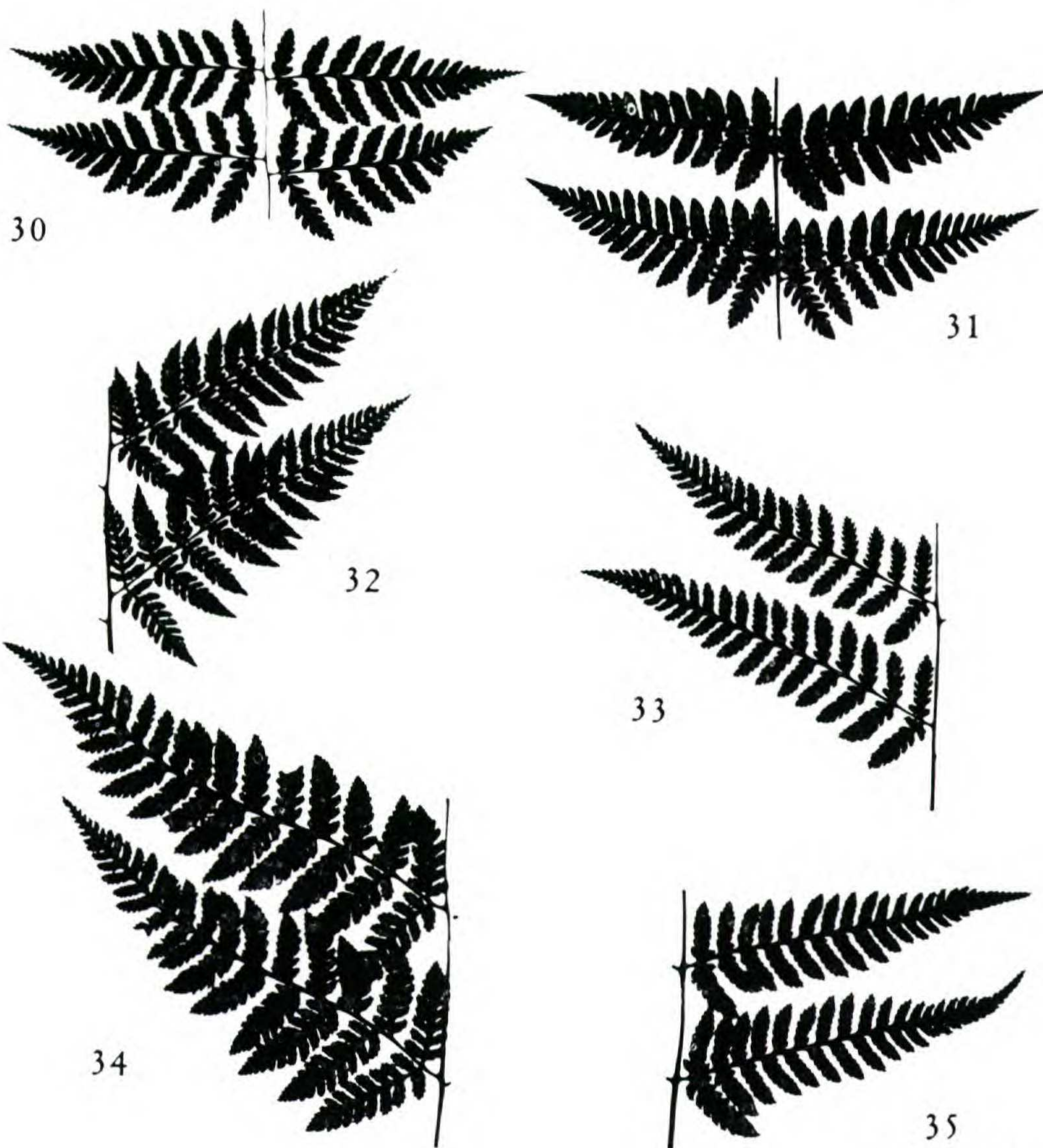


PLATE 1327

Figs. 30-35. Central pinnae of *Dryopteris spinulosa* var. *spinulosa*, tetraploid, $\times 1/3$. Fig. 30 — from Plant 33. Fig. 31 — from Plant 370. Fig. 32 — from Plant 79. Fig. 33 — from Plant 305. Fig. 34 — from Plant 488. Fig. 35 — from Plant 289.

h. Aspect of the lamina.

The aspect of the lamina is usually different in *spinulosa* and *intermedia*. This may be readily observed in fig. 5 of *intermedia* and fig. 9 of *spinulosa* which are characteristic of each taxon. One of the initial objectives of this study was to analyze the general character of aspect into its individual components. This objective was partially but not wholly

realized. Characters *c* to *g* are individual characters of aspect and our analyses of these, therefore, also represent an analysis of aspect. Other individual characters have not been analyzed and among these may be mentioned shape, symmetry, spacing and complexity of the pinnae, of the pinnules and of the tertiary segments, and the length, shape and orientation of the marginal teeth.

Figures 17 to 35 illustrate the central pinnae of leaves that were selected to present the variation in aspect of the three cytotypes. Common aspects of *intermedia* are illustrated by figs. 21 and 23, of the *hybrid* by figs. 25 and 27, and of *spinulosa* by figs. 31 and 35. The other figures of 17-35 represent less common variations. The greatest resemblance of *intermedia* to *spinulosa* is seen in figs. 20 and 34. The aspect of the *hybrid* seems to intergrade with that of both of its parents. Figure 17 of *intermedia* is close to fig. 29 of the *hybrid* and fig. 19 of *intermedia* is close (except in the orientation of the pinnae) to fig. 24 of the *hybrid*. The aspect of the *hybrid* and *spinulosa* is similar in fig. 27 of the *hybrid* and fig. 33 of *spinulosa*, and in fig. 26 of the *hybrid* and fig. 34 of *spinulosa*.

i. Glandularity of the indusium.

Glands of the same type as those on the lamina also occur on the indusium of *intermedia* and the *hybrid*. The indusium of *spinulosa* is glabrous. Eighty-one per cent of the 89 plants of *intermedia* had the indusia definitely glandular and nineteen per cent had them slightly glandular; eighty-five per cent of the 47 plants of the *hybrid* had the indusia definitely glandular and fifteen per cent had them slightly glandular. These observations were made only on the cytological voucher leaves, collected in early summer, since the glands tend to be deciduous with age. However, in both *intermedia* and the *hybrid*, glands were also observed on the indusia of leaves that had lived over the winter.

j. Spores.

Our observations of the spores of numerous plants of *intermedia* and *spinulosa* showed them to be normal in ap-

pearance and presumably viable. Only rarely was an abortive spore seen. The spores of the *hybrid*, on the other hand, were uniformly shriveled (abortive). No normal appearing spores were seen among those of the *hybrid* although some effort was made to find them.

k. Chromosome number.

The chromosome counts, already mentioned, may be summarized here for the sake of a complete list of the characters studied,

intermedia: diploid, $n = 41$ (89 plants).

hybrid: triploid, $n = \frac{123}{2}$ (47 plants).

spinulosa: tetraploid, $n = 82$ (52 plants).

DISCUSSION.

Variation in the cytotypes. —

In relation to the numerical as well as the geographical limitations of our sample, it is desirable that some assessment be made of the parameters of the variation that have been established in our study. An effort was made to obtain a cytological analysis of as many variants as possible and we believe that most of the variation was obtained in the areas sampled. Nevertheless, it is patent from a study of materials in the Gray Herbarium and the Herbarium of the New England Botanical Club that there is greater variability in the *Dryopteris spinulosa* group than in our cytologically determined samples of it. For this reason we are reluctant to place reliance on our parameters as those of the taxa and their hybrid. We feel that most of the parameters can be extended by further cytological sampling, especially in other regions. The means of the characters, however, and the mean of the means, can probably be extrapolated with some confidence as representative of the taxa and the hybrid because of the inertia of the mean.

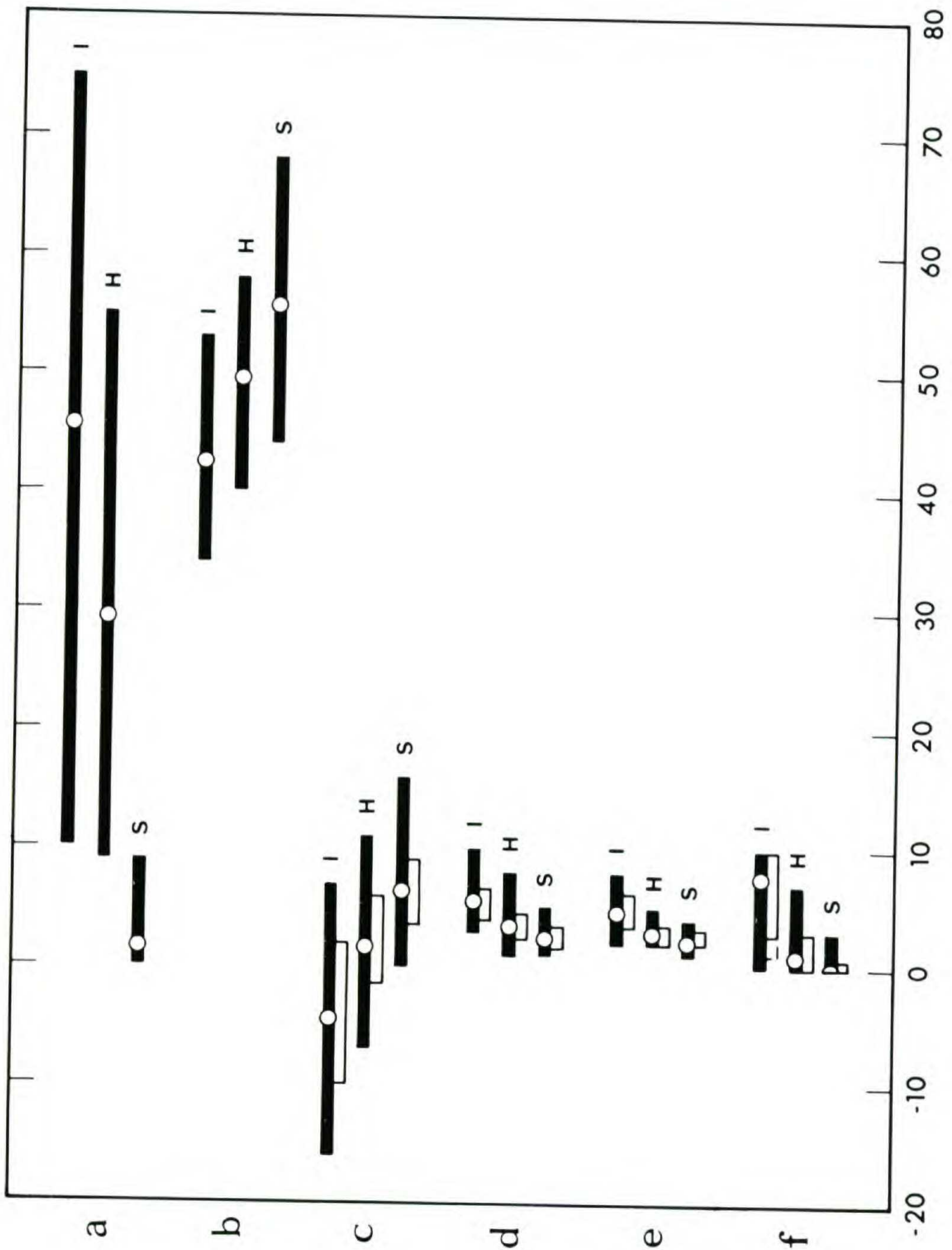
The range of variation of the original counts and measurements is presented in Graph 1. It is portrayed more clearly in Graph 2 where the original data has been adjusted for comparative purposes. Considering the data from all leaves,

CHART 3. Analysis of variation in *Dryopteris spinulosa*, adjusted scores (see text) of characters *a* to *f*. (See Graph 2.)

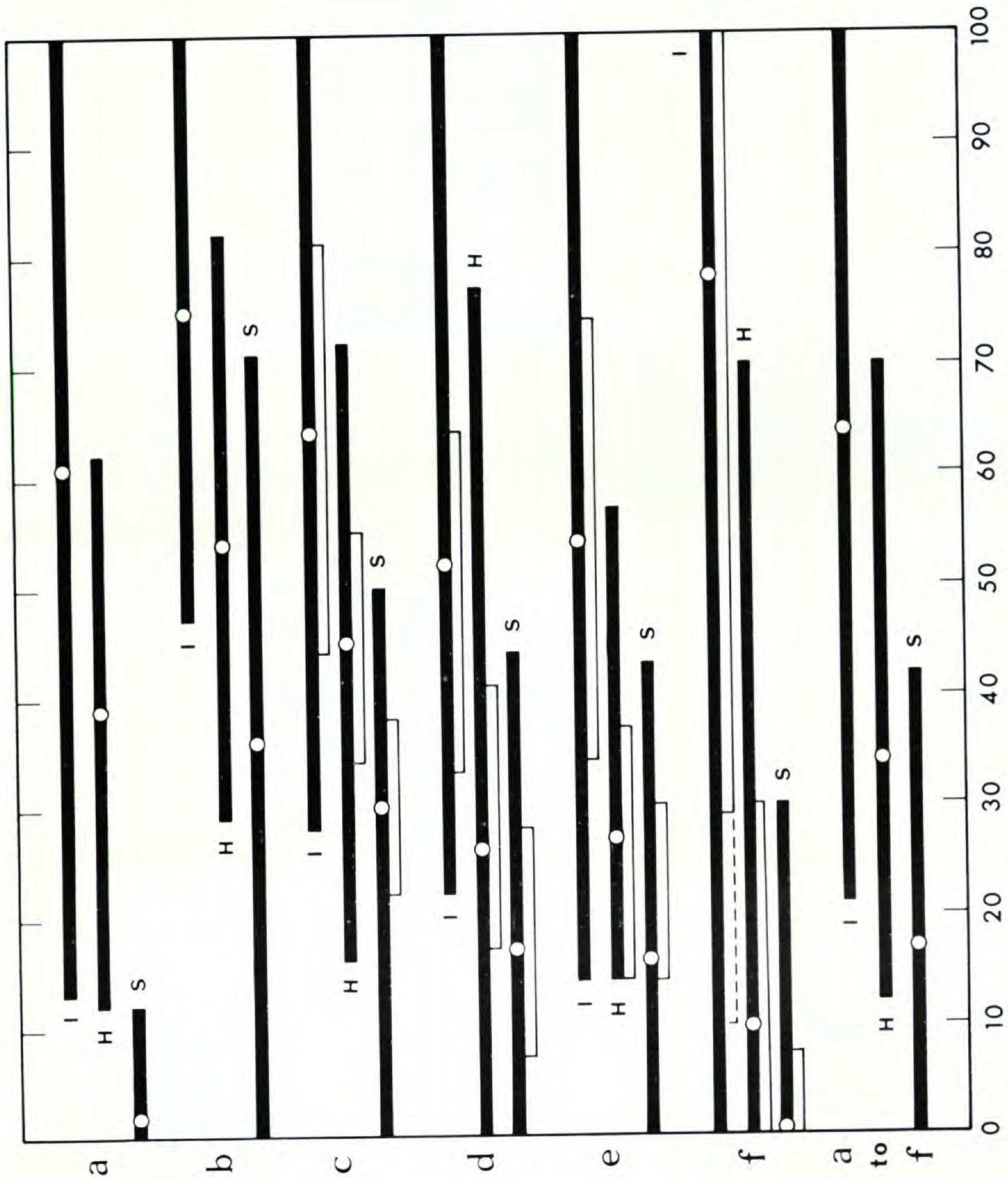
| Character. | | Range of variation. | | Mean of |
|---------------|-------------------|--------------------------|---------------------------------------|----------------|
| | | All leaves. | Mean of plants with 4 or more leaves. | all leaves. |
| <i>a</i> | <i>intermedia</i> | 13-100 | | 61 |
| | <i>hybrid</i> | 12-62 | | 39 |
| | <i>spinulosa</i> | 0-12 | | 2 |
| <i>b</i> | <i>intermedia</i> | 47-100 | | 75 |
| | <i>hybrid</i> | 29-82 | | 54 |
| | <i>spinulosa</i> | 0-71 | | 36 |
| <i>c</i> | <i>intermedia</i> | 28-100 | 44-81 | 64 |
| | <i>hybrid</i> | 16-72 | 34-55 | 45 |
| | <i>spinulosa</i> | 0-50 | 22-38 | 30 |
| <i>d</i> | <i>intermedia</i> | 22-100 | 33-64 | 52 |
| | <i>hybrid</i> | 0-77 | 17-41 | 26 |
| | <i>spinulosa</i> | 0-44 | 7-28 | 17 |
| <i>e</i> | <i>intermedia</i> | 14-100 | 34-74 | 54 |
| | <i>hybrid</i> | 14-57 | 14-37 | 27 |
| | <i>spinulosa</i> | 0-43 | 14-30 | 16 |
| <i>f</i> | <i>intermedia</i> | 0-100 | 10*-29-100 | 78 |
| | <i>hybrid</i> | 0-70 | 0-30 | 10 |
| | <i>spinulosa</i> | 0-30 | 0-7.5 | 0.7 |
| | | Mean range of variation. | | Mean of means. |
| <i>a to f</i> | <i>intermedia</i> | 21-100 | | 64 |
| | <i>hybrid</i> | 12-70 | | 34 |
| | <i>spinulosa</i> | 0-42 | | 17 |

*Plant 357 with two leaves.

it will be seen in Graph 2 that the range of variation (minimum to maximum score) of each cytotype overlaps that of the others in characters *b* to *f*. In character *a*, the range of variation of *intermedia* and the *hybrid* overlap while that of *spinulosa* is contiguous, or nearly so, with the range of those two. The range of variation of the mean of plants with four or more leaves is presented for characters *c* to *f*. In



GRAPH 1. Analysis of variation in *Dryopteris spinulosa*, original counts and measurements of characters *a* to *f*, from Charts 1 and 2. White dot: mean of all leaves. Bars indicate range and extent of variation of a character. Solid bar: all leaves. Outline bar: plant means from plants with four or more leaves (extension by dash of character *f* in *intermedia* includes Plant 357 with only two leaves). I: *intermedia*, H: *hybrid*, S: *spinulosa*.



GRAPH 2. Analysis of variation in *Dryopteris spinulosa*, adjusted scores of characters *a* to *f*, from Chart 3. White dot: mean of all leaves. Bars indicate range and extent of variation of a character. Solid bar: all leaves. Outline bar: plant means from plants with four or more leaves (extension by dashes of character *f* in *intermedia* includes Plant 357 with only two leaves). I: *intermedia*, H: *hybrid*, S: *spinulosa*.

the means of plants the range of variation of *spinulosa* and *intermedia* is discrete in each character, while that of the *hybrid* overlaps the variation of both parents in each of them. The extent of variation (maximum score minus the minimum) of the means of plants is about half that of the extent of the variation of single leaves.

The mean of each character is strikingly different in *spinulosa* and *intermedia*. The mean of the *hybrid* falls between those of the parents. In characters *a* to *c* it is more or less midway between the parental means, while in characters *d* to *f* it is closer to the mean of *spinulosa*. The mean of the means of the six characters demonstrates that, in these, the *hybrid* falls somewhat closer to *spinulosa* than to *intermedia*. We do not wish to imply, however, that this may represent the actual genetic position of the *hybrid* for in other characters it is closer to *intermedia*.

It will be noted also in Graph 2 that in most cases the mean of a character is more or less centrally located between the extremes, while in a few cases it is notably close to one extreme. This is especially true of character *a* in *spinulosa* and of character *f* in all of the cytotypes. The genetic factors which might control these characters would be worthwhile to investigate. At the moment nothing is known of the inheritance of any character in *Dryopteris*. Information concerning numbers of pairs of genes, dominance relationships and factor interaction is lacking.

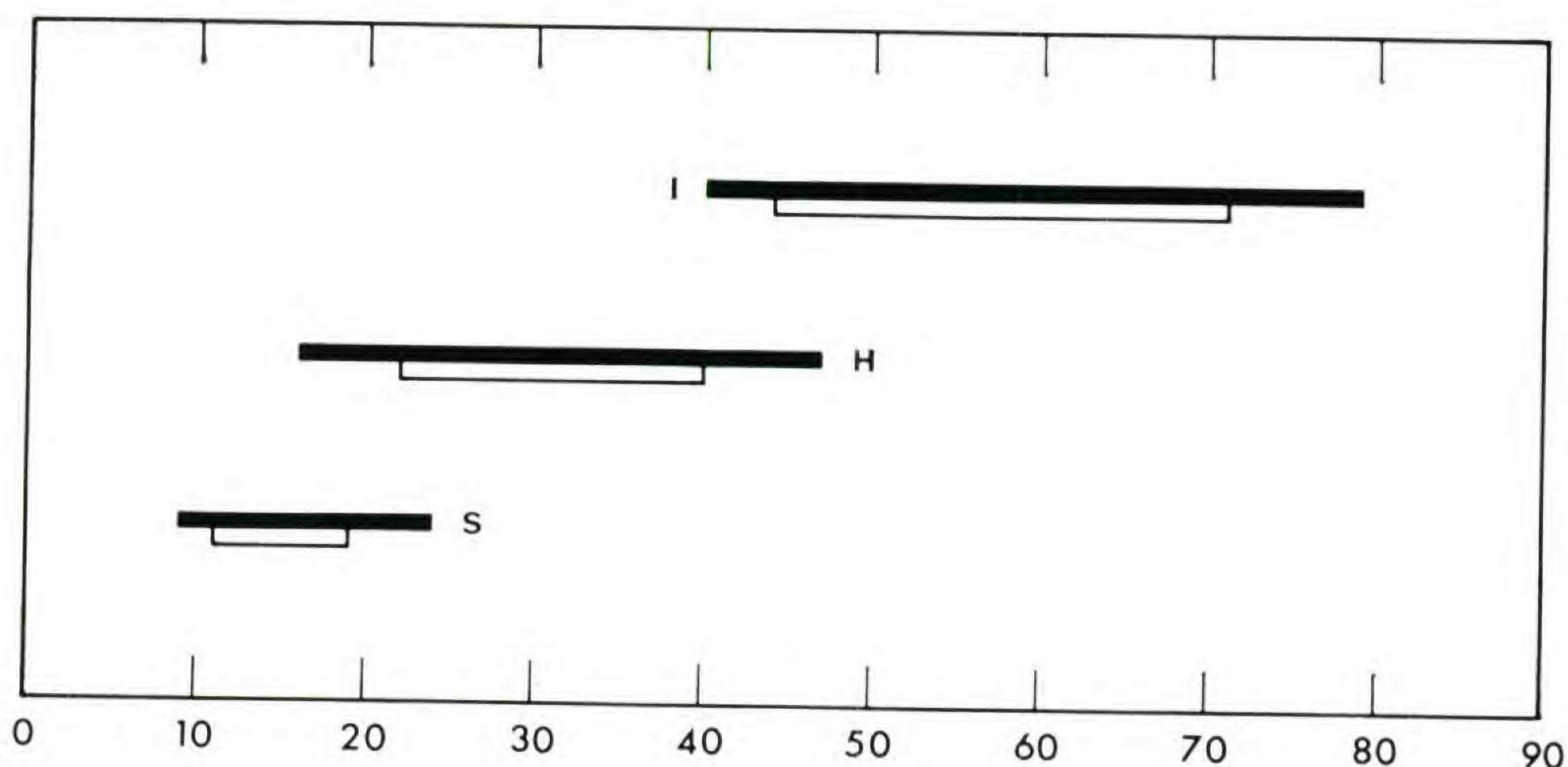
It can be seen in Graph 2 that the extent of variation in a character is usually greater in *intermedia* than in *spinulosa*. In characters *a*, *e* and *f* the extent of variation in *intermedia* is twice as great, or more, than in *spinulosa*. In characters *c* and *d* it is about half again as great in *intermedia* than in *spinulosa*. Only in character *b* is the extent of variation greater in *spinulosa* than in *intermedia*. In each of these characters the extent of variation in the *hybrid* is equal to or greater than that in the less variable parent and smaller than that in the more variable parent. This comparison of variation is summarized in Graph 2 by the bars that indicate the mean range (and extent) of variation of

CHART 4. Analysis of variation in *Dryopteris spinulosa*. Range and extent of variation between extreme leaves and plants in the means of adjusted scores (see text) of characters *a* and *c* to *f*. (See Graph 3.)

| | | Character and score. | | | | | Mean of scores. | Range and (extent) of variation of mean. |
|--------------------|----------------------|----------------------|----------|----------|----------|----------|-----------------|--|
| | | <i>a</i> | <i>c</i> | <i>d</i> | <i>e</i> | <i>f</i> | | |
| <i>inter-media</i> | Leaf from Plant..VJV | 13 | 48 | 33 | 57 | 40 | 40 | 40-79 (39) |
| | Leaf from Plant 104 | 66 | 75 | 78 | 86 | 90 | 79 | |
| <i>hybrid</i> | Leaf from Plant 126 | 12 | 22 | 33 | 14 | 0 | 16 | 16-47 (31) |
| | Leaf from Plant 95 | 44 | 47 | 78 | 57 | 10 | 47 | |
| <i>spinulosa</i> | Leaf from Plant 91 | 0 | 8 | 22 | 14 | 0 | 9 | 9-24 (15) |
| | Leaf from Plant 370 | 0 | 34 | 33 | 43 | 10 | 24 | |

| | | Character and mean of plant | | | | | Mean of means. | |
|--------------------|-----------------------|-----------------------------|----------|----------|----------|----------|----------------|------------|
| | | <i>a</i> | <i>c</i> | <i>d</i> | <i>e</i> | <i>f</i> | | |
| <i>inter-media</i> | Plant 101 4 leaves | 13 | 52 | 33 | 64 | 57 | 44 | 44-71 (27) |
| | Plant 113 4 leaves | 55 | 80 | 56 | 74 | 92 | 71 | |
| <i>hybrid</i> | Plant 284 6 leaves | 12 | 38 | 30 | 29 | 3 | 22 | 22-40 (18) |
| | Plant 116 4 leaves | 73 | 50 | 33 | 36 | 10 | 40 | |
| <i>spinulosa</i> | Plant 36 13 leaves | 3 | 27 | 13 | 14 | 0 | 11 | 11-19 (8) |
| | Plant 43 8 leaves | 5 | 38 | 21 | 30 | 0 | 19 | |

all six characters (mean of the minimum scores to mean of the maximum). The extent of variation is almost twice as great in *intermedia* (79) as in *spinulosa* (42), while in the *hybrid* it is quite intermediate (58) between the two.



GRAPH 3. Analysis of variation in *Dryopteris spinulosa*, range and extent of variation in means of adjusted scores of characters *a* and *c* to *f*, from Chart 4. Solid bar: variation between extreme leaves. Outline bar: variation between extreme plants. I: *intermedia*, H: *hybrid*, S: *spinulosa*.

The greater extent of variation of the characters of *intermedia* is consistent with the opportunities for recombination and mutation to be expressed phenotypically at the diploid level and the smaller extent of variation of *spinulosa* is consistent with the restrictions on their expression at the tetraploid level.

The variation as represented by extreme leaves and extreme plants and the extent of variation between them is given in Chart 4 and in Graph 3. It will be seen that the extent of variation among extreme leaves and extreme plants is more than twice as great in *intermedia* as in *spinulosa* while in the *hybrid* it is about midway between that of the parents. The fact that the extent of variation in individual characters, in extreme leaves and in extreme plants of the *hybrid*, is so nearly intermediate between that of the parents implies that the hybrid plants we have analyzed have come from the whole spectrum of variation of the parent plants as we have seen it.

One of the most interesting aspects of the variation of the cytotypes is their intraplant variability. Data on this variation, from selected plants, are presented in Chart 5.

The last column of the chart gives the extent of the intraplant variation as a *per cent* of the total extent of variation in the cytotype. Most commonly the intraplant variation is rather small and this is illustrated by plants 27 and 301 which show the variation in the leaves of a plant in one year (one crown) and plants 36 and 38 (1959, 1960) which show the variation in the mean of crowns in successive years. The frequent extent of intraplant variation of a character is about 15%, or less, of that of the cytotype. Rarely the intraplant variation may be great and this is illustrated in plants 38 (1959) and 504 which show the variation in the leaves of a plant in one year and plants 32 and 117 which show the variation in the mean of crowns in successive years. These examples illustrate that rarely the extent of variation of a character in one plant may be 70%, or more, of that of the cytotype or, as in plant 117, may even exceed that of the cytotype. (This is due to the fact that in Chart 3 the mean of plants is derived from all available leaves of a plant rather than only those of a single crown.)

The genetic implications of the great intraplant variability suggest that the genes controlling these characters are not markedly different in *intermedia* and *spinulosa*. They also suggest that the expressivity of the genes is extremely variable, providing that no unusual mitotic divisions are involved and that the cells of a plant all have a characteristic genotype. Similar variability in gene expression is well known in other plants, for example, the leaves of *Morus alba*. The taxonomic implications are that it vitiates, to a degree, the differences between the taxa brought out by the difference in their means of these characters.

The only character that we have studied in which no variation was observed within a cytotype was the chromosome number. Although both the spores and the indusia have been grouped into two discrete classes: normal-abortive and glabrous-glandular respectively, there is in fact variation in both of these characters. We have not studied the proportion of normal to abortive spores in *spinulosa* and *intermedia*,

CHART 5. Intraplant variation in *Dryopteris spinulosa*. Range and extent of variation of single characters in selected plants. Data on individual leaves are in roman type, data of means of plants are in *italic*.

| Plant, cytotype and material. | Character. | Range of Variation. | | Extent of Variation In example as % of cytotype. | | |
|---|------------|---|---------------------|---|-----------------|------|
| | | Original data. | Adjusted scores. | In example. | In cytotype. | |
| Plant 301, <i>hybrid</i> , 5 leaves, 1960 | <i>c</i> | 0.5 mm. longer to 3 mm. longer | 41-48 | 7 | 56 | 12% |
| Plant 27, <i>intermedia</i> 4 leaves, 1960 | <i>d</i> | 5 to 6 | 44-56 | 12 | 78 | 15% |
| Plant 504, <i>spinulosa</i> , 4 leaves, 1961 | <i>c</i> | 4 mm. longer to 15 mm. longer | 3-38 | 35 | 50 | 70% |
| Plant 38, <i>hybrid</i> 5 leaves, 1959 | <i>c</i> | 6.5 mm. shorter to 9.5 mm. longer | 20-70 | 50 | 56 | 90% |
| Plant 36, <i>spinulosa</i> , 4 leaves, 1959, 5 in 1960 | <i>c</i> | 7.2 mm. longer in '59 to 7.4 mm. longer in '60 | 27-28 | 1 | 16 | 6% |
| Plant 38, <i>hybrid</i> 5 leaves, 1959, 3 in 1960. | <i>c</i> | 1 mm. longer in '59 to 1.8 mm. longer in '60 | 44-47 | 3 | 21 | 14% |
| Plant 32, <i>hybrid</i> , 4 leaves, 1959, 3 in 1960 | <i>f</i> | 2 in 1959 to 4.3 in 1960 | 20-43 | 23 | 30 | 77% |
| Plant 117, <i>hybrid</i> , 3 leaves, 1959, 3 in 1960 | <i>e</i> | 3.66 in 1959 to 1.66 in 1960 | 9-38 | 29 | 23 | 126% |

being content with the observation that the abortive spores are rare. The glandularity of the indusium of *intermedia* and of the *hybrid* is clearly variable and although this has not been studied in detail it seems to show a range of variation similar to that of the pinna base in *intermedia* and the *hybrid*.

Identification. —

Identification is most readily made during the rather brief time when mature spores are present in abundance. There is a possibility of contamination when there are only a few spores. During this two or three week period, the *hybrid* is readily identified by its abortive spores, *intermedia* by its normal spores and glandular indusium and *spinulosa* by its normal spores and glabrous indusium. Before, or after, this period fertile leaves of *spinulosa* may be identified by their glabrous indusium but *intermedia* and the hybrid cannot be distinguished from each other by the indusium. Sterile material of *spinulosa* or *intermedia* cannot always be distinguished from the *hybrid*. The difficulties of identification, then, center on the many herbarium specimens and plants in nature that are collected or observed at a time when uncontaminated mature spores are not present. Other characters must then be employed, if possible, for identification and it is with these that this study has largely been concerned.

We have mentioned our conclusion that the parameters of the characters we have studied are undoubtedly greater in the taxa and their hybrid than in our sample of them. For this reason we do not believe that any of the data on single characters (Charts 1, 2 and 3, Graphs 1 and 2) afford a basis for the identification of all plants of the cytotypes. In all of the characters, except *a*, the range of variation of one cytotype overlaps that of another (or both) and in character *a*, the range of *spinulosa* is very close to that of the other two.

The data on extreme plants (Chart 4, Graph 3), derived from the mean of 5 characters, shows that the range of variation of each cytotype is distinct from that of the other

two. However, the degree of distinction is small: a difference (in the mean of the adjusted scores) of 3 between plant 43 of *spinulosa* (19) and plant 284 of the *hybrid* (22) and a difference of 4 between plant 116 of the *hybrid* (40) and plant 101 of *intermedia* (44). We do not believe that these small differences afford a basis for the identification of all plants of the cytotypes.

It seems worthwhile to emphasize the variability of character *c*, the relative length of the inferior basal pinnules on the basal pinnae and the adjacent ones, because this character has been much relied upon in the literature for purposes of identification. Chart 2 and figs. 11-12, 15-16 demonstrate the variability in this character. *Intermedia* usually has the inferior basal pinnules shorter than the adjacent ones (fig. 11), but they may be longer (fig. 12) and *spinulosa*, usually has the basal inferior pinnules longer than the adjacent ones (fig. 16), but they may be equal in length (fig. 15). The great variation among the leaves of one crown can be seen in Chart 5, Plant 38 (1959) in which one of the five leaves had the inferior basal pinnules 6.5 mm. shorter than the adjacent ones and another leaf had them 9.5 mm. longer.

The evergreen quality of the leaves has also been emphasized in the literature and it is generally true that leaves of *spinulosa* are deciduous and those of *intermedia* are evergreen. However, our limited observations have indicated that this character is a variable one especially influenced by the environment of the individual plant. In most of the plants of the *hybrid* that were studied the leaves were deciduous or only partially evergreen but in some they were evergreen as is typical *intermedia*.

Other characters employed in the identification of the taxa and their hybrid that we have also found to be too variable to be utilized are the position of the pinnae in relation to the rachis (see Analysis of Characters, *g.*) and the aspect of the lamina (see Analysis of Characters, *h.*). Considering the variability discovered in all of the characters mentioned, we feel that others such as the orientation of

the rhizome, the color of the petiole scales and the type of spines on the spores cannot be accepted as affording a distinction of the taxa until their constancy has been confirmed by an extensive study of plants of known identity.

There remain then as wholly applicable characters for identification of the cytotypes only the glandular or glabrous indusium, the abortive or normal spores and the chromosome number. Certain extremes of other characters do seem sufficiently distinctive to allow some confidence in their use and these have been added to the key. It will be obvious that the key will not allow the identification of all material.

Key.

Indusium glandular.

Spores normal; $n=41$. (Any leaf with 9-10 basal inferior pinnules on the lowest 10 pinnae overlying the rachis, or any plant with four or more leaves averaging 6-10 overlying pinnules probably belongs here.) *intermedia*
 Spores abortive; $n=123$. (Any plant with a glandular in-

2

..... *hybrid*
 dusium and four or more leaves averaging 0 overlying pinnules probably belongs here.) *hybrid*

Indusium glabrous; spores normal; $n=82$. (Any leaf with the pinna-bases glabrous probably belongs here.) *spinulosa*

Classification. —

The authors are in amiable, but firm, disagreement about the proper taxonomic status of *intermedia* and *spinulosa*. Donald M. Britton is of the opinion that, in these taxa, the cytogenetic evidence must be decisive. *Intermedia* is a basic diploid taxon genetically isolated from *spinulosa* which is a derived polyploid taxon. Accordingly, the status of species is most appropriate for each of them. Rolla Tryon is of the opinion that the taxonomic status of *intermedia* and *spinulosa* must be determined by a comparison of the two to each other and to other taxa in their alliance on the basis of all evidences of similarity and difference. He is of the opinion that the similarities and differences brought out in the present study make the category variety most appropriate, at the same time admitting that this status is tentative pending adequate comparative studies of other allied taxa.

It is difficult to decide whether or not the *hybrid* should be treated as a taxon and then be designated by a binomial. Rather than explore this complex question here we prefer not to recognize it as a taxon but to formally refer to it by the appropriate formula. This is advantageous because it directly conveys the parentage which is the most important information about a hybrid.

The triploid hybrid. —

There are several aspects of the natural history of the sterile *hybrid* that deserve some additional discussion. Although its distribution is not well known, its presence has been cytologically confirmed in Ontario, Massachusetts, New Jersey, Virginia and Michigan. It is probably to be found throughout northeastern United States and adjacent Canada within the range of the two parents and in most localities where they both grow. We have found it at all (seven) localities where cytological sampling revealed the presence of both *intermedia* and *spinulosa*. In Massachusetts, it has been found at each of several localities where a search was made for it. Most of these plants were identified by their abortive spores; a few were identified by their chromosome number. The data in Chart 6 suggest the abundance of the *hybrid* in a few localities and also demonstrate how it may be more abundant than either parent. We have observed in the same locality that the triploid plants often have larger leaves and more leaves than those of the parents. While this might be due to environmental conditions that are more favorable for it than for either parent, it seems more likely that it is due to the phenomenon of hybrid vigor.

The hybrid plants may arise in two ways. The plant may come from the fertilization of a gametophyte of one parent by one of the other parent, or it may come from an existing plant by vegetative reproduction. Although we have seen some evidence of clonal development in the *hybrid* we have not been able to assess the relative importance of this in the formation of populations. The principal reason being that although a close similarity of plants that are near each other may be taken as evidence of a clone, it does not follow

CHART 6. Relative abundance of *Dryopteris spinulosa* at four localities, from random samples of the populations.

| Locality. | Number of plants. | % of population. |
|--|-------------------|------------------|
| 'High and Dry', Wellington Co., Ontario. | | |
| <i>intermedia</i> | 16 | 19 |
| <i>hybrid</i> | 56 | 65 |
| <i>spinulosa</i> | 14 | 16 |
| Cockburn Swamp, Wellington Co., Ontario. | | |
| <i>intermedia</i> | 3 | 11 |
| <i>hybrid</i> | 14 | 52 |
| <i>spinulosa</i> | 10 | 37 |
| Sodom, Halton Co., Ontario. | | |
| <i>intermedia</i> | 16 | 31 |
| <i>hybrid</i> | 20 | 38 |
| <i>spinulosa</i> | 16 | 31 |
| Littleton, Massachusetts. | | |
| <i>intermedia</i> | 26 | 27 |
| <i>hybrid</i> | 62 | 64 |
| <i>spinulosa</i> | 9 | 9 |

that dissimilar plants always represent independent hybrids. The data in Chart 5 on variation in a crown from one year to the next (plants 32, 117) are sufficiently suggestive of the variability that may be present in a clone to make its identification in the field most uncertain.

Some estimate of the extent of clonal development may be made by measuring the growth of the rhizome apex. The growth of the adult rhizome extends the apex some two or three centimeters a year and when the apex occasionally branches two separate plants are soon produced. Lateral stolons are also commonly produced from between the persistent leaf bases, on the older portions of the rhizome. These are slender and grow three or four centimeters in length before the internodes shorten and a crown of small leaves is produced. The base of the stolon soon dies and the rhizome of the small separate plant then may spread away from the parent. The spread of a clone by these two methods is rather slow and it would not occupy more than fifty to a hundred square meters of area in a few hundred years.

In many localities where the *hybrid* grows, it occupies an area of several thousand square meters. Even allowing

for maximal clonal development, each of these large populations must represent a few dozen, or even a few hundred, original hybrid plants. Such populations must occur frequently over an extensive area, at least from Virginia to New England, Ontario and Michigan, and they must represent several hundred thousand F_1 plants.

This frequency of crossing of the parental gametophytes can be evidence of the breeding behavior of the parents themselves. Since the gametophytes of the two taxa can cross with some frequency, those from different plants of the same taxon should do so with equal or greater frequency. Although we do not have sufficient data on the population structure of *intermedia* and *spinulosa* to bring to bear as evidence of predominant outcrossing, our data on variation are consistent with the idea that outcrossing occurs. It seems appropriate to bring out this indirect evidence for relatively frequent outcrossing since so little is known about the natural breeding behavior of ferns.

The relative greater abundance of the *hybrid* than either parent (Chart 6) is unusual, perhaps unique, in sterile hybrid ferns. Most of these in *Dryopteris* are rare and occur only as an occasional plant or small colony in a very few of the places where the parents grow together, for example, *D. marginalis* \times *spinulosa* var. *intermedia* and *D. Goldiana* \times *marginalis*. A few are more common and occur in many localities where both parents grow, for example, *D. cristata* \times *spinulosa* and *D. cristata* \times *spinulosa* var. *intermedia*. The latter, perhaps more familiar as *D.* \times *Boottii*, is the most common hybrid, except for *intermedia* \times *spinulosa*, but it is never as abundant as its parents. We believe that the great abundance of *intermedia* \times *spinulosa* is due to the large number of hybrid sporelings that are formed and to their intermediate physiological traits. Their physiology may adapt them to a large number of niches favorable for immediate survival. It may also provide them, and older plants, with the capacity to survive drought and pluvial periods, that might diminish the numbers of *spinulosa*, which prefers wet conditions, and also of *intermedia*, which prefers drier ones.

When we first became aware of the frequency of the *hybrid*, we fully expected that further sampling would reveal a hexaploid. Although this expectation was not realized there are some aspects of the triploid hybrid that have a pertinence to studies of naturally occurring hexaploids. One of these aspects is the proximity of extreme plants of the *hybrid* (Chart 4 and Graph 3) to certain plants of the parents. A hexaploid produced from one of these plants would be much closer to one parent than to the other and if the triploid became extinct (or was unknown) the relations of the hexaploid might be correspondingly obscured. Further difficulties in the analysis of the hexaploid would result if it were produced more than once and from plants at the opposite ends of the spectrum of variation of the triploid.

The origin of the tetraploid. —

The hybrid of *spinulosa* and *intermedia* has approximately 41 pairs of chromosomes and 41 single chromosomes and on the basis of this evidence, Walker (1961) has concluded that the parents share a common genome. Therefore, he considers *spinulosa* to be an allopolyploid with *intermedia* as one of its ancestral parents. Among the known diploids only *intermedia* is a credible parent for *spinulosa* and, if *spinulosa* is an allopolyploid, it is evident that the other parent is either extinct or is as yet undetected. It must also be considered, however, that *spinulosa* may be an autopolyploid between two members of an original diploid *spinulosa* taxon which was closely related to *intermedia*.

There are two characters of *spinulosa* that are not consistent with Walker's hypothesis. These are the glabrous indusium and the only slightly and infrequently glandular lamina. A hybrid with typical *intermedia* would be expected to have a glandular indusium and a more glandular lamina as, for example, in *D. cristata* × *spinulosa* var. *intermedia* and in *D. cristata* var. *Clintoniana* × *spinulosa* var. *intermedia*. However, it must be admitted that we can not be certain that the glandularity of *intermedia* is always strongly dominant in its hybrids and so the slight

glandularity of *spinulosa* can only be a qualified objection to Walker's hypothesis.

Our data on the breadth of variation in *intermedia*, and in the *hybrid*, suggest that Walker's interpretation may be correct under certain circumstances. The present data would be sufficiently consistent with his hypothesis if one of the parents of the original hybrid *spinulosa* were a plant of *intermedia* that was rather distant from the central variation of the taxon in the direction of *spinulosa*. It would also be consistent if one of the parents of the original hybrid *spinulosa* was a member of an ancestral *intermedia* that was closer to the present *spinulosa* and which has since diverged from it.

The variation that we have observed in *spinulosa* and in *intermedia* suggests that the origin of *spinulosa* may be a complex problem and that further studies are desirable to substantiate the claim of *intermedia* as one of its parents.

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